ALIMENTARY CAECA OF AGNOSTIDS AND OTHER TRILOBITES

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ABSTRACT. Genal and other caeca of trilobites have left distinctive imprints of veins and lines on the test; all such 'ornamental lines and veins' are referred to as 'alimentary prosopon'. In agnostids the alimentary prosopon consists of scrobiculae and rugae; the genal caeca of agnostids form a left and a right reniform ramified gland, connected with the glabella (oesophagus) by one or two pairs of short diverticula. The caeca are few and relatively thick, and reticulation is scant. The scrobicules probably correspond to mesenteries, and the preglabellar frontal furrow probably corresponds to a median mesentery. The frontal sulcus probably indicates that the front of the oesophagus was bilobed. The pygidial caecal apparatus of agnostids is similar to that of the cephalon. The alimentary apparatus of agnostids is similar to that of *Burgessia*.

In *Redlichia* and olenellids the genal caeca consist of radiating and anastomosing capillary vessels, whereas in the fixed cheek, including the palpebral lobes, ingluvial sacs replace the caeca. In *Redlichia* each segment of the thorax bears two pairs of veins, which are regarded as intestinal appendages (caeca or diverticula).

In ptychopariids (*Papyriaspis*) the genal caeca are of capillary size; the ocular ridges consist of two pairs of lines, interpreted as diverticula, with the palpebral lobes and the eye at their tips. The caecal veins of the postero-lateral border terminate in a swelling (opistopleural terminal glandular swelling). Each segment of the thorax bears two pairs of intestinal appendages, and the anterior segments possess as well the 'glandular swelling' at the tips of the pleurae. The intestinal appendages are probably homologous with the ocular ridges, and the opisto-pleural swellings with the eyes. The anterior part of the pygidium repeats the structure of the thorax; in the posterior part of the pygidium the segments fuse and the caeca radiate, anastomose, and reticulate, and so repeat the pattern of the genal caeca. This is also demonstrated on the pygidium of an undescribed ptychopariid, and a pleura of *Centropleura* shows structures similar to those described in ptychopariids.

Trilobites have segmentally arranged intestinal appendages; their eyes are segmental and located at the tips of a pair of pleurae; caeca are developed only on the pleural lobe; and the cephalic, frontal, border, and doublure including the rostral shield are pleural elements and not part of the axial lobe.

As examples of agnostids with well-developed cephalic and pygidial caeca *Glyptagnostus* and its two species—*reticulatus* (Angelin) and *stolidotus* sp.nov.—are described. The caecal prosopon of *G. stolidotus* consists of conspicuous rugae, and the cephalic and pygidial glands are almost mirror images of one another.

INTRODUCTION

THE aim of the present paper is a description of the alimentary glands known in the literature as 'genal caeca' of trilobites. The material is arranged in two parts: first, the principal morphological observations and interpretations are presented, and, secondly, the results are tested in the taxonomy and morphology of *Glyptagnostus*.

The segmental arrangement of caecal glands, their presence in all tagmata, and their duplication in each segment, are the main results of the study. A new trilobite model can be visualized when the present results are combined with ideas concerning the origin of the pygidium and the hypostoma, and the pleural nature of the rostral shield (Öpik 1958). A preliminary note has already been published (Öpik 1959).

Observations on the anatomy and organization of trilobites are steadily accumulating, and, hand in hand with this progress, theories arise on the origin, phylogeny, and progeny of trilobites. It becomes increasingly evident that trilobites are neither Crustacea nor Merostomata, although they are commonly interpreted by comparison with the latter. In the present study a somewhat different approach has been attempted: Cam-

brian trilobites are studied here solely on their own merits, and post-Cambrian trilobites (and possible relatives and descendants) are not taken into consideration because they had no influence on Cambrian life and its evolution. Of course, trilobites are here regarded as arthropods, and the general organization of arthropods is considered in the interpretation of the observations.

The morphology of trilobites is not yet known completely, for the obvious reason of incomplete preservation. Still, recent finds of well-preserved material have provided more information; in particular, the cuticular sculpture, which is termed the 'alimentary prosopon', is exceptionally well preserved in the Australian material, which has been collected in undisturbed rocks without any trace of metamorphism. The term 'alimentary prosopon' refers to traces of the cephalic caeca and their homologues on the thorax and the pygidium. The alimentary prosopon is in effect a map of the pleural alimentary apparatus of trilobites.

G. Lindström, P. E. Raymond, C. D. Walcott, A. Born, R. Richter, and L. Störmer are the main contributors to the knowledge of the alimentary apparatus of trilobites. The most recent summary of current knowledge is given by Hupé (1953a, pp. 82–84) as follows: the glabella contains the oesophagus, from which caeca extend into the cheeks and the frontal limb; the intestine, which has no lateral ramifications, extends from the rear of the oesophagus along the axis of the thorax and the pygidium. He also refers to the observation by Volborth of a metamerized intestine in *Illaenus*.

Hupé also suggests that the genal caeca emerge from the oesophagus and are connected to it by diverticula. He (1953a, p. 81, fig. 35) assumes that at the maximum development of metamerization the head of a trilobite is equipped with four pairs of diverticula with ramified caeca. The foremost pair are the ocular ridges. The caeca of the frontal limb emerge direct from the front of the glabella, i.e. from the anterior end of the oesophagus.

The observations here presented confirm Hupé's theory of the connexion of the genal caeca with the oesophagus, and the function of the ocular ridges as alimentary diverticula.

The Australian Cambrian trilobites, however, permit some amplification of Hupé's description of the cephalic alimentary apparatus of trilobites in general. Thus, the frontal caeca extend on to the marginal border; the ocular ridge is a double ridge and its distal extension is the double palpebral lobe; the ocular ridge represents not a single diverticulum, but a double pair of diverticula and, consequently, not four but five pairs of diverticula probably existed.

Furthermore, the posterior marginal border of the cephalon carries two pairs of diverticula, and the veins of the posterior pair terminate in the form of a 'glandular swelling' or opistopleural terminal swelling. The frontal caeca probably emerge not from the oesophagus but from the anterior ocular ridge, the extension of which is the 'parafrontal band' in front of the glabella.

Cephalic caeca can be regarded as established in trilobites. Post-cephalic caeca in the thorax and pygidium, which have so far escaped the scrutiny of palaeontologists, can now be added to the model of the trilobite.

Diverticula (intestinal appendages) are regularly arranged on the pleurae of the thorax and pygidium; each segment bears two pairs of them. In trilobites with a developed pygidial border and progressive fusion of the pleural segments towards the rear, the posterior portion of the pygidial pleural platform bears caeca that are similar to the

cephalic caeca. These new observations on the occurrence of post-cephalic alimentary prosopon have been made on the ptychopariid *Papyriaspis* (thorax and pygidium); *Olenus, Redlichia,* and *Centropleura* (thorax only); and on the dolichometopid *Amphoton*, and in *Proceratopyge* (ramified caeca on pygidium).

All that is preserved of the alimentary diverticula and caeca are their moulds on the inner surface of the test that appear externally as low ridges and lines. As each mould is usually more pronounced than the corresponding outer line, the observed pattern simply reflects the external structure of the soft parts of the trilobite body. To use a term proposed by Gill (1949), the pleural alimentary apparatus of trilobites manifests itself as an alimentary 'prosopon' of the test.

The ornament of trilobites consists of terraced lines, lines, netting, granules, pits, and puncta. This external ornament, if well enough developed or if the test is thin, may also be reflected on the internal surface of the test. But the external ornament is, of course, more pronounced on the external than on the internal surface and thereby differs fundamentally from the alimentary prosopon.

The two pleurae of *Centropleura* (Pl. 68, figs. 3, 4) illustrate the difference. In fig. 3 the test is preserved with its external 'ornamental' lines, and the opistopleural vein only is indicated. The pleura in fig. 4—a rubber cast of the parietal (internal) surface—shows the opistopleural and propleural veins, whereas the external lines are only partly impressed, perhaps by compaction pressure of the sediment.

The preservation of the details of the alimentary prosopon is not always clear on untreated fossils and may escape detection. For better results the calcareous test is washed with ordinary soap and a nylon toothbrush.

With some rare exceptions noted by Hupé, Ordovician and younger trilobites lack the alimentary prosopon. But, presumably, more examples will be found if diligently searched for. The pleural alimentary apparatus of most Ordovician and younger trilobites was probably 'deep-seated', not in touch with the parietal surface, and therefore did not produce any cuticular sculpture.

Heavy surface ornament or a thick test usually masks the alimentary prosopon. Trilobites with a thin smooth test preserved in limestone yield the best results. However, specimens of a single species from the same bed differ because within the soft body of different individuals the position of the caeca may vary in relation to the parietal surface: caeca that are deep-seated in one individual may lie near the surface in another.

The alimentary prosopon may be preserved in shale as well. For example, steinkerns of *Redlichia*, preserved in siliceous shale and chert (Öpik 1958, pl. 4; pl. 6, figs. 4, 6), show the pleural lines (intestinal appendages).

Modern methods of whitening fossils for study and photography, and appropriate magnification of printed illustrations, facilitate the study and presentation of the details of the alimentary apparatus. A good example is the illustrations of the olenid *Acerocare tullbergi* in Henningsmoen (1957, pl. 30, fig. 9), which shows pleural lines similar to those of *Redlichia*.

AGNOSTIDS

The scrobiculate test of agnostids. In many agnostids the cheeks have grooves that radiate from near the dorsal furrows. Authors have termed such cheeks scrobiculate, wrinkled, furrowed, grooved, rugose, or covered with ramified furrows or with ribs and

furrows. Well-illustrated examples can be examined in Westergaard (1946). In some agnostids with an apparently smooth test the grooves can be detected when whitening is applied. Grooves are lacking in a few agnostids only.

Scrobiculation and caeca. The diagrams (text-figs. 2–4) illustrate the common scrobiculate pattern of the head of agnostids. This pattern is regular and is bilaterally symmetrical; it has been observed in many species of several genera. It signifies the existence of a pair of dendritic ramified glands under the test of the cheeks of the agnostid head connected with the glabella (containing the stomach) by one or two pairs of short ducts (diverticula). The glands usually surround the front of the glabella but do not meet; in *Hypagnostus* (text-fig. 3), however, the frontal glabellar lobe (stomach) is obsolete, but appears to be replaced by a duct connecting the glands. In one form (*Corrugatagnostus*, text-figs. 5, 6) a radiating arrangement occurs as a variation of the fundamental dendritic pattern. As shown below, these glands are homologous with the genal caeca of other trilobites. The caeca of agnostids are characterized by their relatively small number of ramifications, the dendritic arrangement, and the relatively large diameter of a single caecum (exceeding capillary size).

In a few agnostids the pleural lobes are scrobiculate in both shields. These include several species of *Pseudagnostus* Jaekel—especially *P. securiger* (Lake)—*Oidalagnostus* Westergaard, *Lotagnostus* Whitehouse, and *Glyptagnostus* Whitehouse (Pl. 70). More familiar is the combination of a scrobiculate cephalon with a smooth pygidium.

To explain the absence of scrobiculation in the pygidia of some agnostids, we note that all agnostids should have caeca even in the absence of an external prosopon; accepting this, it should follow that in the cephalon of some forms the caeca have a relatively shallow position near the parietal surface and produce a cuticular sculpture, whereas in pygidia of the same forms the caeca are mostly deep seated and produce no external caecal prosopon.

The pygidia of such forms are convex and provide ample space to accommodate the glands below the surface. *Corrugatagnostus* Kobayashi (text-figs. 5, 6), however, has a relatively flat pygidium and therefore shows a well-developed caecal prosopon. This, however, is not the only possible solution. For example, agnostids that have scrobiculate pygidia (*Oidalagnostus* and *Pseudagnostus*; *Lotagnostus* and *Glyptagnostus*; *Corrugatagnostus*) constitute three separate groups, each of a relatively late geological age (uppermost Middle Cambrian, Upper Cambrian, and Ordovician). Each of these three groups could have acquired, independently from the others, their ramified pygidial caeca as a modification of an earlier, simpler form of glands. The earlier, Middle Cambrian, agnostids have smooth pygidia; and therefore in the early agnostids the pygidial caeca may have had a form that was incapable of producing an external prosopon, and need not have been simply 'deep seated'. In this case, the pygidia would have had lateral ingluvial sacs only, and no ramified glands.

Comparison with Burgessia. The idea that the scrobiculate pattern of the agnostid test is an alimentary prosopon is illustrated by comparison of the carapace of *Burgessia* Walcott (text-fig. 1) with the cephalon of *Diplagnostus* (text-fig. 2). As *Burgessia* has no pygidium, the comparison refers only to the cephalon of agnostids and the carapace of *Burgessia*.

Burgessia is an arthropod with a carapace and is definitely not an agnostid trilobite.
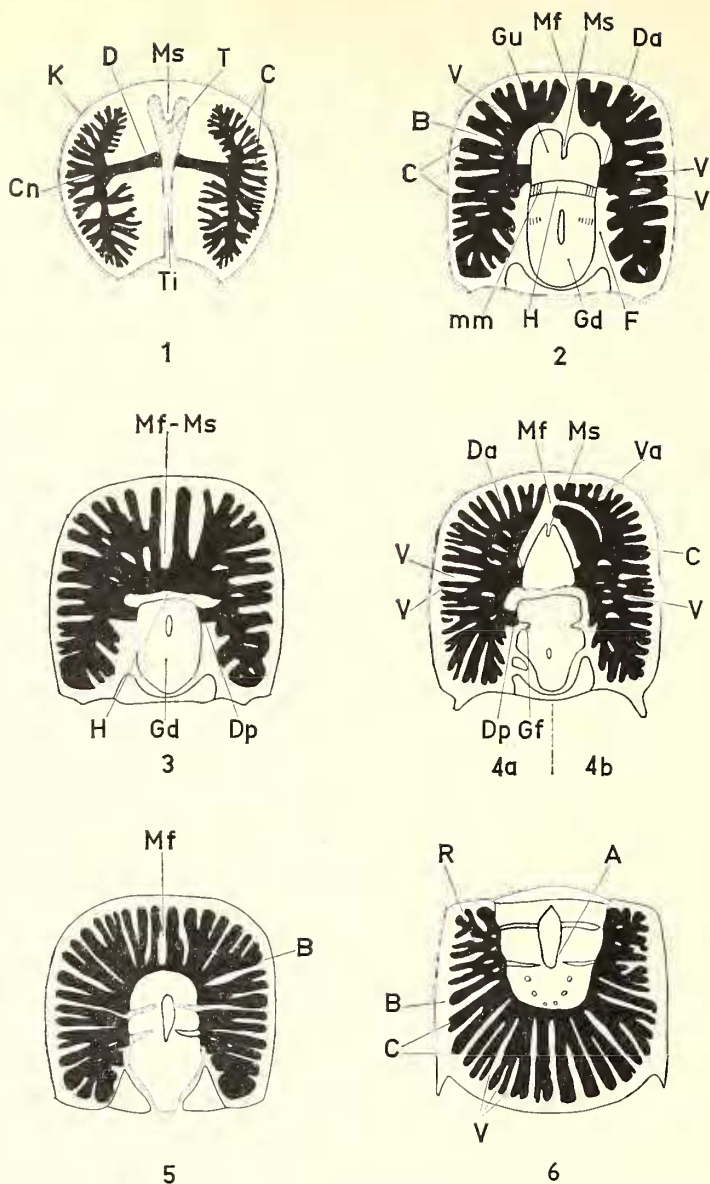
TEXT-FIGS. 1–6. Diagrams of the alimentary apparatus of *Burgessia* and agnostids. 1, *Burgessia* Walcott 1912. Anterior part, a simplified interpretation. After Walcott (1931). 2, *Diplagnostus*. Cephalon, based on Scandinavian (Westergaard 1946, pl. 8) and Australian specimens. 3, *Hypagnostus*. Cephalon, based on *H. exsculptus* (Angelin). Adapted from Westergaard (1946, Pl. 6, fig. 1). 4, *Ptychagnostus*. Cephalon, combined from several illustrations in Westergaard, and some Australian specimens. The left half (4a) shows two pairs of diverticula; the right half (4b) shows one pair of diverticula and arcuate scrobicules. This serves also as an explanation of *Tomagnostus*, *Glyptagnostus*, &c. 5, 6, *Corrugatagnostus*. Adapted from Whittard (1955). 5, Cephalon; 6, Pygidium. A—axial lobe (pygidium); B—border with doublure; C—caeca (rugae); Cn—caecal node; D—diverticulum; Da—anterior diverticulum; Dp—posterior diverticulum; F—dorsal (axial) furrow; Gd—posterior lobe of glabella; Gf—glabellar furrow (lateral indentations); Gu—anterior lobe of glabella; H—transverse glabellar furrow; K—outline of carapace (in *Burgessia*); Mf—preglabellar median furrow (mesentery); mm—muscle spots (in H); Ms—frontal sulcus; R—reticulation; T—stomach; Ti—intestine; V—scrobiculae (mesenteries); Va—arcuate scrobicule.

In *Burgessia*, however, the alimentary apparatus itself is preserved and is not known only from imprints on the test. The apparatus consists of a bifurcated stomach, an intestine, and a pair of dendritic reniform glands—the ramified caeca. A bifurcate stomach is shown (text-fig. 1) in accordance with the text in Walcott (1931, p. 18), although Walcott's diagram shows an 'anterior central lobe of the stomach', i.e. a trilobate stomach. Walcott's interpretation in the text is preferred to the alternative indicated in his illustration.

The alimentary apparatus of *Diplagnostus* (text-fig. 2) differs from that of *Burgessia* (text-fig. 1) in the following characters:

1. The diverticula are long in *Burgessia*, short in the agnostid—a minor difference.
2. In *Burgessia* the stomach lies in front of the diverticula and the intestine behind it, whereas, in the agnostid, behind the diverticula lies the posterior lobe of the glabella that, presumably, also contains a part of the stomach—a major difference.
3. Similar bilateral caecal glands are accommodated under the carapace of *Burgessia*, and under the cephalic shield of the agnostid; but the carapace of *Burgessia* covers 'five cephalic, eight thoracic, and one abdominal segment', whereas in the agnostid the cephalic shield alone covers a similar apparatus—a fundamental difference.

In my opinion the caecal glands of *Burgessia* and of the agnostid are homologous in form and position, and in relation to the stomach, and are functionally identical. But still a difference remains, because, as indicated above, in the agnostid the glands are confined to the cephalon, and in *Burgessia* they have expanded beyond the cephalon.

Furthermore, the carapace of *Burgessia* is externally non-lobate; but internally it is divided into an axis provided with the alimentary canal and 'pleural' lateral lobes provided with caecal glands; consequently, *Burgessia* is in this sense internally trilobate and is comparable with the agnostid trilobite.

The similarity of the alimentary apparatus of *Burgessia* to the cephalic alimentary apparatus of the agnostid suggests that both kinds of animals have retained the same ancestral design of the alimentary apparatus, though they remain far apart in other aspects of their organization. On the other hand, the apparent simplicity of the alimentary apparatus of *Burgessia* and of the agnostid, and not common descent, may be the cause of the similarity. Metabolism and digestion are primary functions and presumably all ancestral animals had a similar simple alimentary apparatus. For such reasons the anatomy of the digestive organs may have little meaning in the problem of a possible phylogenetic relationship between *Burgessia* and agnostids.

Within the class of the trilobites, however, which includes the uncomplicated agnostids and the more complicated ptychopariids, the diversity of the organization of the alimentary apparatus is probably of some phylogenetic significance. Thus, agnostids may have retained a primitive and, therefore, ancestral alimentary system, from which the complicated system of other trilobites was derived. This, of course, is no indication that agnostids are ancestors of the others.

Morphology of the caecal glands of agnostids. The alimentary prosopon of agnostids is manifested as a wrinkling of the pleural lobes. The wrinkles consist of radiating swells or rugae, separated by furrows or scrobiculae. The scrobiculae are narrow and sharp, and have been regarded by taxonomists as the substantial element of the wrinkled ornament of agnostids. But the wrinkling and its regular and recurrent radiating

arrangement is already a hint that some organs existed that have produced the 'ornament'.

The rugae are channels and the scrobiculae narrow crests on the internal, parietal, surface of the test. In turn, these parietal channels are moulds of the caeca. The crests are partitions (parietal septa) between the caeca and probably served as carriers of membranous mesenteries.

The scrobicules (parietal septa) are often discontinuous, especially at a distance away from the margin, and produce externally a pitted pattern, whereas near the margin of the test they are continuous and radial. The rugae also more or less radiate along the margin and may reticulate near the centre of the cheek: thus, the caeca in the cheeks of agnostids are roughly reticulate, and the cheeks may be pitted. Still another form of reticulation occurs in *Glyptagnostus* and is described below.

The preglabellar median furrow separates the left and right caecal glands from one another. This furrow, a crest on the inner surface, indicates a median parietal septum and a corresponding mesentery that separates and keeps in place the caeca. In some agnostids this furrow is externally effaced, or almost so, but it is indicated by a crest on the internal surface. In most species of *Peronopsis*, and in some other forms, the preglabellar median furrow is absent altogether, but this does not necessarily imply the absence of a median mesenterial partition. The external absence of some organs may mean that they are absent altogether, as, for example, the absence of eyes certainly means blindness, but the absence of an external manifestation of a mesentery that has a mechanical function is no indication of its total absence. In smooth agnostids (e.g. *Grandagnostus*) even the external trilobation is absent, but internally such forms still remain 'trilobed' trilobites. In taxonomy, incidentally, the absence or presence of the median preglabellar furrow has been regarded as a character of generic and even family significance.

The traces of one or two pairs of diverticula can be observed in the cephalon of agnostids (text-fig. 4), and are referred to as anterior and posterior diverticula.

The best published examples of the anterior and posterior cephalic diverticula in one specimen can be selected from Westergaard (1946) as follows: *Leiopyge laevigata perrugata* (pl. 14, fig. 2), *Diplagnostus planicauda vestgothicus* (pl. 8, fig. 26), *Ptychagnostus atavus* (pl. 11, fig. 13), *Cotalagnostus lens claudicans* (pl. 6, fig. 25), and *Hypagnostus exsculptus* (pl. 6, fig. 1).

The traces of diverticula are not visible in all specimens; their definition depends not only on the preservation of the fossil, but also on their erratic external manifestation. They occur as 'bars' crossing the dorsal furrows; the outer ends of these bars are the nodes from which the caeca radiate, and the nodes themselves have a fixed position. The bars may be strong, weak, or missing altogether, presumably because one diverticulum or another may dive under the parietal crest of the dorsal furrow instead of crossing it straight and forming a bar. The anterior diverticula always arise from the posterolateral flanks of the anterior glabellar lobe, and the posterior ones from immediately in front of the anterior glabellar furrows (lateral indentations) of the posterior lobe.

The fixed position of the diverticula and their connexion with the caecal nodes, which also maintain a fixed position, is proof that organization and not chance or accident determines the distribution of the alimentary prosopon of the agnostids.

The glabella, from which the diverticula branch off, is assumed to have contained the oesophagus (proventriculum, stomach), because no other space is available for its

accommodation. The glabella consists of two main lobes (anterior and posterior) separated by the transverse glabellar furrow. This furrow presumably constricted the stomach from above, and muscles attached to the outer ends of the furrow constricted the stomach laterally. In other words, the stomach of the agnostid probably consists of an anterior and a posterior sac or cavity connected beneath the transverse furrow by a constricted passage.

The posterior sac is evidently a relatively late acquisition, and is an ingluvies formed by an enlargement of the original anterior portion of the intestine. No direct evidence can be produced in support of this assumption, but the following reasoning is pertinent:

1. Agnostids are trilobites.
2. In the trilobite *Redlichia* (Öpik 1958), for example, the four posterior lobes of the glabella display occipital similarity, and, therefore, in the ancestors of *Redlichia*, the posterior four segments of the cephalon were probably added gradually, and existed at some stage as freely articulating segments.
3. Features preserved in some agnostids (furrows, muscle spots) indicate that the posterior lobe of the glabella also consists of four segments; and by analogy with other trilobites the transverse glabellar furrow apparently belongs to the foremost of these four segments.
4. The transverse glabellar furrow is probably a vestigial segmental division, and a relic of an articulation joint between two segments or two tagmata—the original head and thorax of an arthropod ancestral to the agnostids. Hence, the anterior, frontal lobe of the glabella, to which the four posterior lobes were added, may represent the original stomach. In some agnostids (*Diplagnostus*, *Tomagnostus*, *Glyptagnostus*, and, sporadically, *Ptychagnostus atavus*) the frontal lobe bears a frontal median sulcus, probably indicating a waning bilobation of the front of the oesophagus that is well developed in *Burgessia*. The same conclusion remains in force when this sulcus is regarded as the extension of the median frontal furrow with its mesentery.

Discussion of examples. *Diplagnostus* (text-fig. 2) has already been discussed and compared with *Burgessia*, and therefore needs no further comment.

Hypagnostus (text-fig. 3) embraces species of agnostids that have a waning or obsolete frontal lobe of the glabella. The obsolete frontal lobe probably indicates a reduction of the original stomach, and a transfer of its functions to the posterior sac of the stomach. This, however, cannot be assumed to be true in every case of effacement of the frontal lobe, because a single effacement of the external relief of the test is no indication of loss of organs. The reduction of the anterior sac of the stomach is apparent only if the place of the frontal lobe is occupied by the scrobiculae and rugae of the caecal prosopon. In our example, *Hypagnostus exsculptus* (Angelin), the frontal caeca are as strong (prominent) as those on the flanks, and the place of the frontal lobe is completely covered by them. But no evidence is available of the loss of the passage (duct) below the transverse furrow, connecting the posterior sac (glabellar cavity) with the frontal caeca.

Condydopyge, with its expanded anterior lobe, is an example of a tendency opposite to that of *Hypagnostus* (see Westergaard 1946, pl. 2, fig. 1). The same trilobite, by the way, clearly exemplifies occipital similarity.

The caecal pattern of *Ptychagnostus* and *Tomagnostus* is shown in text-fig. 4. In these forms the distal caeca are finer and more numerous than in *Hypagnostus*; diverticula (one pair, or two pairs) are present; and a frontal sulcus occurs in *Tomagnostus*, and sporadically in *Ptychagnostus*. A pair of arcuate scrobicules accentuates the bilateral symmetry of the distribution of the glands.

In *Corrugatagnostus* (text-figs. 5, 6) the frontal lobe of the glabella is probably

obsolete. The frontal preglabellar furrow (the median mesentery), as illustrated, for example, by Whittard (1955, pl. 1, fig. 12), is present. The pygidial caeca of *Corrugatagnostus* are almost a replica of the cephalic pattern, and the anterolateral pygidial caeca are reticulate. The scrobiculae that radiate inwards from the margin are almost straight.

Glyptagnostus stolidotus sp. nov. provides an example of ramified pygidial caeca and is described separately below.

Efficiency of the agnostid alimentary apparatus. The kind of food of agnostids is as yet unknown, as are their cephalic and other appendages. The small size of agnostids, their universal distribution in various sediments, and their abundance in bituminous rocks indicate that they fed on microbios. The convex carapace and relatively large and spacious cheeks and pleural lobes of the pygidium contained voluminous caecal glands. These glands accommodated amounts of food, the weight of which probably exceeded the weight of the agnostid body itself, and which should have lasted for some time. On the other hand, it is also possible, but less probable, that the caecal glands were so large because the nutritive value of the food was low and had to be compensated by volume. Nevertheless, and in spite of their blindness, it is improbable that agnostids were benthonic mud-eaters.

REDLICHIA AND OLENELLIDS

In *Redlichia* and in several olenellids, authors have noted a 'confluence' of the palpebral lobes with the frontal lobe of the glabella, and a 'confluence' of the two posterior glabellar lobes with the swollen fixed cheek. In *Redlichia forresti* 'the cephalic dorsal furrows are deep at their junction with the glabellar furrows and shallow in contact with the glabellar lobes' (Öpik 1958, p. 26). These 'shallow contacts' are bars across the dorsal furrows and are interpreted here as sites of lateral diverticula. These bars (diverticula) may either interrupt the dorsal furrows almost completely, or remain inconspicuous, or even be invisible, and this variability may occur in a single specimen. The diverticula apparently did not remain rigidly at a definite level, but varied in depth below the cuticle within certain limits. When the diverticula were shallow the dorsal furrow was interrupted, whereas deeper-seated diverticula passed under the furrow without forming a bar across it. The 'confluence of lobes' and the swollen fixed cheek, and the two pairs of swellings in the cheeks seen in some olenellids, can be explained by assuming that the diverticula terminated in the form of ingluvial sacs located between the dorsal furrows and the eye. Of course, such ingluvies could have been encased in tissue that was itself penetrated by delicate caeca; however, in *Olenellus* and *Redlichia* no radiate or reticulate caecal prosopon is seen in the space between the eye and the glabella.

The outer cheeks and the brim of olenellids, like those of ptychopariids, bear radiating capillary caecal veins which have their source at the base of the eye and the front of the glabella. The same is also shown in the diagram of the cephalon of *Redlichia* (text-fig. 8), although in some species of the genus the caecal veins are not only ramified but also reticulate.

A special variation of caecal pattern of *Redlichia* is the presence of a pair of facial lines on the brim. Öpik (1958, p. 31) suggests that the facial lines and the lines on the pleurae of *Redlichia* may represent vestiges of similar organs. If so, they are alimentary caeca,

and 'the facial lines, consequently, may indicate the position of pleural elements within the otherwise fused cephalon'. Because of some instability of the facial lines they were regarded as ornament by Öpik. Actually they belong to the alimentary prosopon of *Redlichia*, as suggested by Hupé (1952, p. 268), who regards them as genal caeca.

Nothing as yet is known about the intestinal appendages of the thorax of olenellids, but observations are available for the related *Redlichia*. According to Öpik (1958, p. 31), veins occur on each side of the pleural furrow. Each segment of the thorax has two pairs
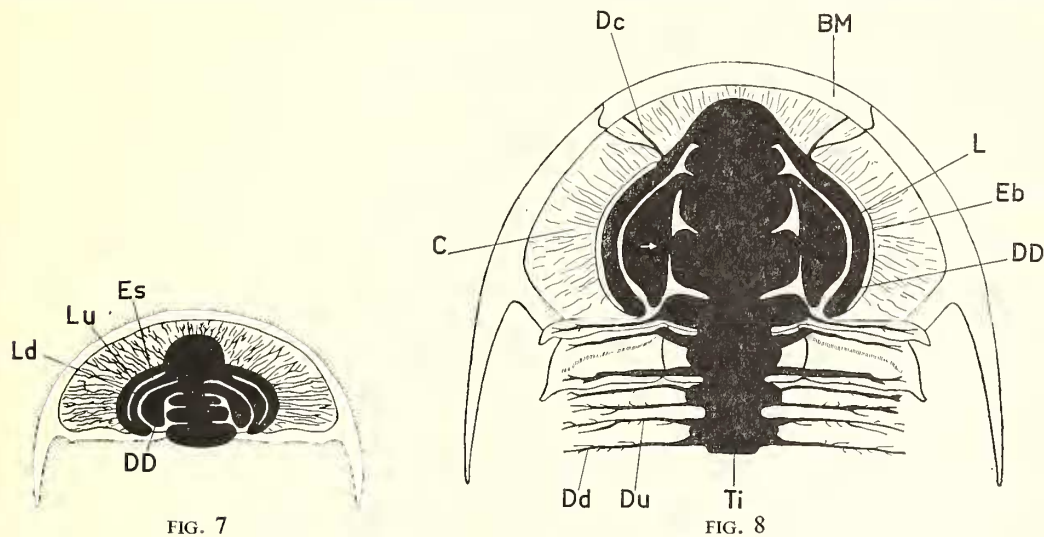
FIG. 7   FIG. 8

TEXT-FIG. 7. Cephalon of an olenellid (*Paedeumias*). Adapted from Öpik (1937, p. 130). DD—diverticular ingluvies; Es—ocular striga (palpebral furrow); Ld—inner palpebral lobe, an ingluvies; Lu—outer palpebral lobe.

TEXT-FIG. 8. *Redlichia*. Cephalon and anterior part of thorax. Outlines adapted from Öpik (1958). BM—border (rim) of cranidium, with rostral shield (ventral); C—capillary genal caeca; Dc—facial line (diverticular vein homologous with Dd or Du); DD—ingluvies (swelling of fixed cheek) connected with oesophagus (glabella) by two pairs of diverticula (arrow on left side indicates one of them); Dd—opistopleural vein (intestinal appendage); Du—propleural vein (intestinal appendage); Eb—base of eye; L—palpebral lobe; Ti—intestine.

of veins, in accordance with similar structures seen in *Papyriaspis* (see below). In the diagram (text-fig. 8) these lines are interpreted as slightly ramified intestinal appendages (caeca) issuing from the intestine.

The intestine is assumed to be annulated by analogy with the lobate oesophagus (glabella), and because such lobation conforms with the external shape and internal structure of the tergites; the constrictions of the intestine also correspond to the position of the apodemes at the junction of the somites.

PTYCHOPARIIDS (*PAPYRIASPIS*)

Plate 68, figs. 1, 2; Plate 69, fig. 1; text-figs. 9–13

Present state of knowledge. Ptychopariids are a large group of trilobites that were spread over the seas of the globe in the Cambrian Period. Unlike the agnostids they are multi-segmented, and most of the species have eyes. The caecal prosopon is preserved in many

of these fossils. Indeed, the present knowledge of the caeca of trilobites is based on ptychopariids. The most complete diagram of cephalic caeca is given by Hupé (1953A, p. 83), for *Ptychoparia striata* Emmrich from the Bohemian Middle Cambrian. Hupé's schematic reconstruction of the alimentary apparatus of trilobites (1953A, p. 81) is also based on ptychopariids and represents the view that caeca were restricted to the cephalon and that they were present only on the cheeks (genal caeca) and the frontal brim.

Hupé correctly shows that the caeca were connected with the oesophagus by at least (or by the maximum number of) four pairs of lateral diverticula. The ocular ridges constitute the anterior pair of these diverticula.

The observations of *Papyriaspis*, as presented below, allow for amplifications and modifications of this picture; an observation of special interest is that caeca are present on the pleurae of all tagmata of the trilobite.

Geological origin of the material. The present study is illustrated by examples of *Papyriaspis lanceola* Whitehouse 1939. *P. lanceola* occurs in the upper levels of the Middle Cambrian of Queensland and is associated with *Ptychagnostus punctuosus* (Angelin) and *P. nathorsti* (Brögger). The specimens here illustrated were collected from the V-Creek Limestone at locality M418, about 3 miles east of Morstone, in the Undilla Basin. Particulars of the geology of the area are given in Öpik (1956, 1960).

The rock (V-Creek Limestone) is a fine-grained impure (argillaceous) limestone, well laminated and almost as fissile as shale. Many of the fossils are, therefore, partly flattened, but minute details of the test are nevertheless preserved.

Two photographs (Pl. 68, fig. 1; Pl. 69, fig. 1) illustrate the mode of preservation of *Papyriaspis* in the V-Creek Limestone. Pl. 68, fig. 1, shows the cranidium and the anterior segments of the thorax with all the details shown in text-figs. 9–12. The test of this specimen is slightly corrugated, apparently by differential compaction of the sediment, and the duplication of the ocular ridges is somewhat obscured by a wrinkle. The present of two pairs of these ridges, however, has been established in numerous other specimens.

The pygidium (Pl. 69, fig. 1) was selected because it was found on the same piece of limestone as the specimen shown in Pl. 68, fig. 1; but it is preserved without distortion, except for flattening of the pleurae.

The cranidium illustrated in text-fig. 12 (a tracing from a photograph of a rubber cast) was collected at V-Creek Crossing. In this figure the missing parts of the right posterolateral limb are reconstructed from the left.

Text-figs. 9 and 10 (pleura and pygidium) are tracings from a photograph of a complete specimen from locality M418.

Pleural caeca of Papyriaspis. The description and discussion of the alimentary prosopon

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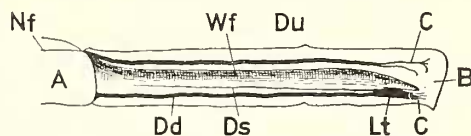ÖPIK, Middle Cambrian trilobites

of *Papyriaspis* should start with the thorax, and especially with its segments, because (1) the segments of the thorax are the simplest units of the tergite, and (2) they display features that have not yet been described. Moreover, the nomenclature applied to the segments of the thorax can be used with advantage in describing the pygidium and the cephalon.

Text-fig. 9 illustrates the structure of a pleura of a thoracic segment of *Papyriaspis*, and of ptychopariid trilobites in general.

The pleural furrow divides the pleura into two separate lobes: an anterior propleuron and a posterior opistopleuron. The lobes are unequal and each has a vein (caecal vein) with a distinctive shape. These veins are regarded here as the prosopon of the intestinal appendages. The veins extend from the dorsal furrow almost to the inner edge of the doublure (*Papyriaspis* has a very narrow doublure). The propleural vein arises at the anterior end of the dorsal furrow; it is wavy

TEXT-FIG. 9. *Papyriaspis lanceola* Whitehouse. Pleura of ninth segment of a complete specimen. A—axial lobe; B—border with doublure; C—terminal caeca; Dd—opistopleural diverticular vein (intestinal appendage); Ds—subsidiary caecal vein; Du—propleural diverticular vein (intestinal appendage); Lt—opistopleural (terminal glandular) swelling; Nf—articulating furrow (homologous with occipital furrow); Wf—pleural furrow.
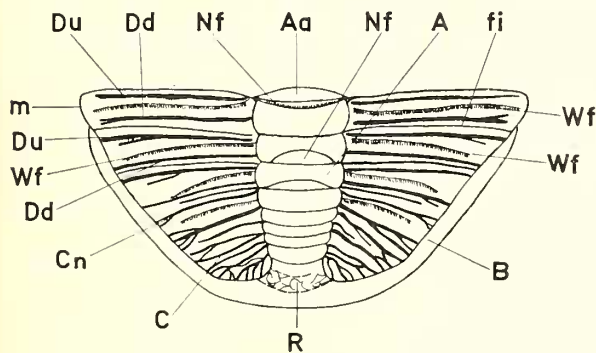
and has a ramified termination. Delicate veinlets branch off the main vein along its posterior slope, but are not shown in the diagram.

FIG. 10

FIG. 11

TEXT-FIG. 10. *Papyriaspis lanceola* Whitehouse. Pygidium anchylosed with last segment of thorax. Adapted from a complete specimen (the same as text-fig. 9). A—axial lobe; Aa—articulating half-ring; B—border with doublure; C—ramified caeca; Cn—caecal node (ramification starts here); Dd—opistopleural vein (intestinal appendage); Du—propleural vein (intestinal appendage); fi—interpleural groove (intersegmental joint); m—margin of anchylosed segment; Nf—articulating furrow; R—reticulate caeca; Wf—pleural furrow.
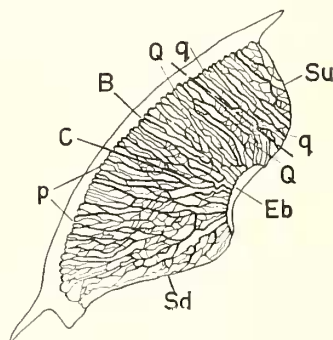
TEXT-FIG. 11. *Papyriaspis lanceola* Whitehouse. Free cheek (Pl. 69, fig. 1). B—border with doublure and, probably, with a caecal trunk; C—capillary-size and ramified genal caeca; Eb—base of eye; p—pits (interspaces between ends of caeca); Q—lateral field; q—anterior field; q/Q—dividing line (caecal 'lineament') between Q and q; Sd—posterior branch of facial suture (posterior edge of free cheek); Su—anterior branch of facial suture (anterior edge of free cheek).

The opistopleural vein has two branches. The main (posterior) branch arises near the posterior end of the dorsal furrow; it is also wavy and has fine veinlets. It terminates in

an elongate swelling, the terminal opistopleural glandular swelling, which has veinlets on its outer end. Between the main branch and the pleural furrow runs the subsidiary vein; it dies out before reaching the dorsal furrow but terminates in the opistopleural swelling.

The opistopleural swellings are strongest on the first segment of the thorax and gradually decrease in size towards the pygidium. From about the middle of the thorax (ninth or tenth segment) the swellings and the subsidiary vein are not discernible.

Pygidial caeca of Papyriaspis. In the pygidium (Pl. 69, fig. 1; text-fig. 10) the first three pleurae repeat the structure of the pleurae of the thorax; over the posterior half of the pygidium, the ends of the veins branch increasingly towards the rear, and over the same area the pleurae fuse completely and the pleural furrows and interpleural grooves disappear. Thus, the veins persist in a ramified and irregularly reticulate pattern similar to that of genal caeca as seen in the free cheek (Pl. 68, fig. 9).

Around the terminus of the axis the reticulate pattern prevails, with narrow pit-like meshes.

The veins of the pleurae of the thorax and of the pygidium are referred to as intestinal appendages or caeca because (1) the veins of the thorax and the pygidium are homologous, and (2) the ramification of the veins on the pygidium increases towards the rear, and the final pattern resembles that of the genal caeca. Each vein with its ramified caeca has a comparable example in the head of the same trilobite (text-fig. 12). As the pygidium has no eyes and no ocular ridges its caecal pattern should be compared with that of blind ptychopariids, as for example *Elyx latifrons* Angelin (see Hupé 1953a, p. 83) or *Dasometopus breviceps* (Angelin) (in Westergaard 1950).

Thus, the thoracic and pygidial veins are morphologically and topologically similar to the genal caeca and therefore probably functioned in the same way.

Assuming, however, that the pygidial caeca are unrelated to the alimentary apparatus, one has to assume the same for the genal caeca, because the complete similarity of the veins and their arrangement on the head and the pygidium suggest a uniform explanation for both.

In summary, alimentary diverticula, caeca, or intestinal appendages in trilobites are present in the cephalon, in the thorax, and in the pygidium. In the thorax and in the pygidium they are arranged segmentally, and two pairs of intestinal appendages belong to any one segment.

This arrangement ought to be expected, because of the metamerism of the trilobite body. An organization in which alimentary caeca issue from the oseophagus only is, however, feasible in arthropods and Crustacea that have a carapace as, for example, *Burgessia* (text-fig. 1).

Cephalon of Papyriaspis. The complete caecal prosopon is preserved in the cephalon of the ptychopariid *Papyriaspis* (Pl. 68, fig. 1). The tracing of the prosopon (text-fig. 12)


EXPLANATION OF PLATE 69

Fig. 1. *Papyriaspis lanceola* Whitehouse, a pygidium, outer surface of the test, × 6. Middle Cambrian V-Creek Limestone; Loc. M418, near Morstone, north-western Queensland. (CPC 577.)

Fig. 2. Pygidium of a ptychopariid (new genus), outer surface of the test, × 12·5. Upper Cambrian Georgina Limestone; Loc. W42, south of Glenormiston, western Queensland. (CPC 578.)
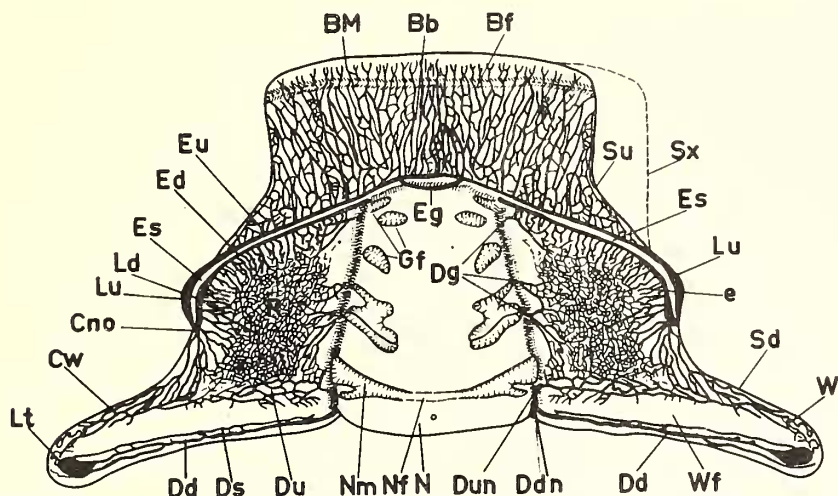
1

2

ÖPIK, Cambrian trilobites
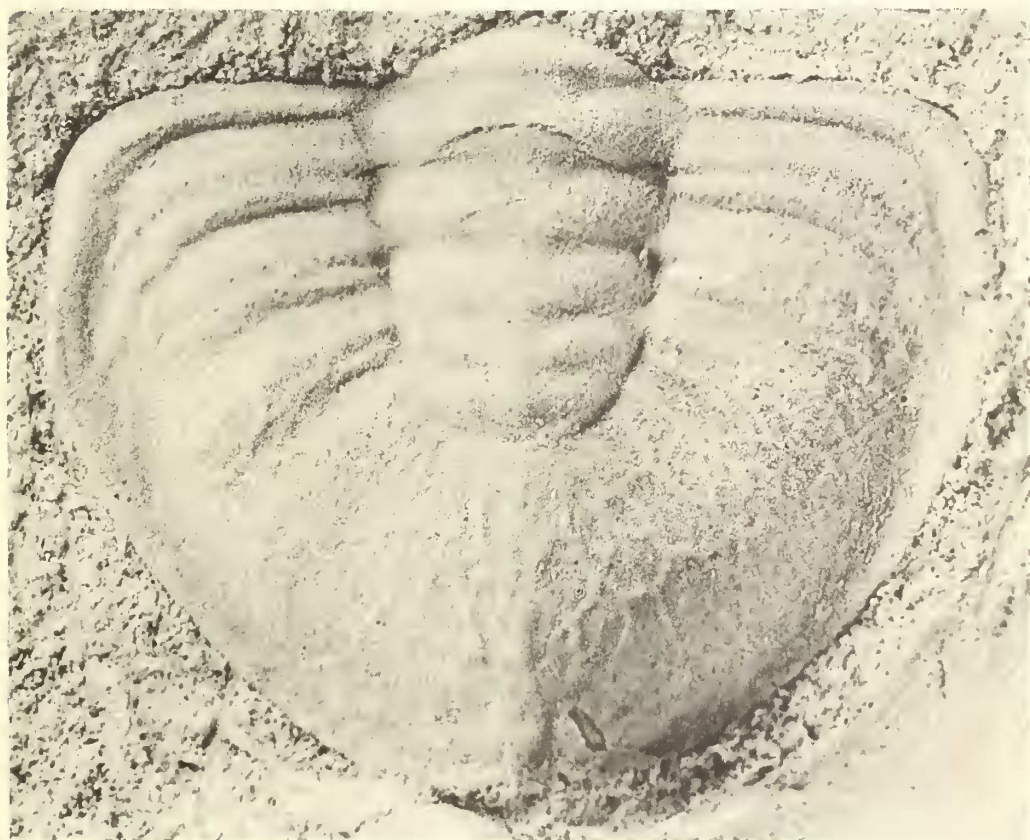
was made from another specimen (not illustrated). This tracing is simplified because the numerous minute veins of the reticulate portions are too fine and dense to be presented in a diagram of convenient size. The free cheek is seen in Pl. 68, fig. 2, and its tracing in text-fig. 11.

TEXT-FIG. 12. *Papyriaspis lanceola* Whitehouse. Cranidium. Tracing from a photograph of an isolated cranidium. Bb—brim with ramified and reticulate capillary caeca; Bf—marginal frontal furrow; BM—rim (border) with ramified caeca and with doublure (no rostral shield in *Papyriaspis*!); Cno—postocular caecal node; Cw—ramified caeca of posterolateral limb (not crossing the suture); Dd—occipital opistopleural vein; Ddn—occipital opistopleural diverticulum; Dg—glabellar diverticula; Ds—subsidiary vein; Du—occipital propleural vein; Dun—occipital propleural diverticulum; e—palpebral furrow; Ed—posterior ocular ridge; Eg—parafrontal band; Es—ocular striga; Eu—anterior ocular ridge; Gf—glabellar furrows (and muscle spots); Ld—inner palpebral lobe; Lt—opistopleural (terminal glandular) swelling; Lu—outer palpebral lobe; N—occipital ring (axial lobe); Nf—occipital furrow; Nm—occipital muscle spots; R—reticulate capillary caeca on fixed cheek; Sd—posterior branch of facial suture; Su—anterior branch of facial suture; Sx—normal position of anterior branch of facial suture in ptychopariids; W—posterolateral limb; Wf—posterolateral (pleural) furrow.

The following peculiarities in the distribution of caeca of the free cheek (genal caeca) are noted:

1. A division into frontal and lateral fields. The caeca of the frontal field cross the suture from the brim; these caeca arise at the anterior ocular ridge. The caeca of the lateral field arise at the base of the eye (at the base of the visual surface); these caeca do not cross the posterior branch of the suture.
2. All genal caeca merge into the thickened border of the cheek as if the border contained a peripheral trunk. The pits along the inner margin of the border are the interspaces between the extreme ends of the caecal veins (Pl. 68, fig. 2). Similar pits are present also in the marginal frontal furrow of the cranidium.

The cranidium (Pl. 68, fig. 1; text-fig. 12) of *Papyriaspis* has a peculiar character not seen in other known ptychopariids: the anterior branches of the facial sutures are markedly concave, and not subparallel, convex outward, or divergent, as in other ptycho-

pariids. At the same time the caecal veins of the brim are not parallel to, or limited by, the suture, but extend across it and continue, as observed above, into the anterior field of the free cheek. The dividing line between the anterior and posterior fields of the free cheek indicates a 'most probable' position of the anterior suture in ptychopariids in general. In *Papyriaspis*, however, the sutures deviate from this position.

Of course, we cannot expect the caecal veins to be strictly parallel to the sutures, because the sutures and the caeca are different features without any common function. We should, however, expect to find a roughly common direction of caeca and sutures among ptychoparids, for this, mechanical, reason: the sutures are lines of weakness, and the direction parallel to the caecal veins is mechanically weaker than that across them. An example of almost exactly parallel suture and caecal veins is seen in *Loganopeltoides zenkeri* (Billings) (Rasetti 1945, pl. 1, fig. 2).

The cranidial caeca behind the eye, along the posterior branch of the facial suture, do not cross the suture. In other words, the posterior suture follows the caecal lineament. So, the position of the anterior branch of the suture in ptychopariids is presumably variable within genera and species, whereas the position of the posterior branch (and, therefore, the shape of the posterolateral limbs) appears to be a conservative character. This conclusion, however, needs the support of a larger number of observations.

Two different kinds of diverticula can be seen in the cranidium of the ptychopariid *Papyriaspis*: (1) the axial diverticula that are located at the dorsal furrows, and (2) those of the ocular ridges. The axial diverticula can be discussed in two groups: (*a*) glabellar diverticula located at the flanks of the glabella, and (*b*) occipital diverticula that arise at the outer ends of the occipital lobe.

Three pairs of glabellar diverticula are present. They arise at the glabellar furrows as ramified bundles that rapidly multiply their branches and merge into a unified reticulate network on the fixed cheeks.

Two pairs of occipital diverticula (veins) are discernible: an anterior ('propleural') pair in front of the marginal furrows and a posterior ('opistopleural') pair, forming the crests of the posterior borders. Each of the posterior diverticula passes into a pair of veins that have the appearance of pleural intestinal appendages.

The anterior veins extend almost to the tips of the posterolateral limbs; the offshoots of these caeca merge into the reticulation of the fixed cheeks. They are referred to as propleural in text-fig. 12 because they occupy the same position relative to the marginal furrow as the propleural veins of the thoracic segments relative to the pleural furrow. All propleural veins probably represent homologous intestinal appendages.

The posterior, opistopleural, veins of the cranidium are exact replicas of the opistopleural veins (including the subsidiary vein) of the anterior pleural segments of the thorax (cf. text-figs. 9, 12). The opistopleural swellings of the cranidium are prominent and are situated at the tips of the posterolateral limbs, which are, therefore, identified as the tips of the occipital pleurae. Hence, occipital similarity is well represented morphologically in *Papyriaspis* and is expressed as a complete segmental homology between the thorax and the occipital segment.

The palpebral lobes, the ocular ridges, and the parafrontal band (a term introduced by Hupé 1953, p. 263) constitute a single diverticular system. Hupé interpreted the parafrontal band as the vestige of a segment (segment 'x'), the pleurae of which are seen in the ocular ridges. It should be noted that the parafrontal band has a median position,

because of which the 'band' could be interpreted itself as being axial and, therefore, part of the glabella. It is, however, an element of the brim and of the pleural lobe in general.

In *Papyriaspis* the parafrontal band is variable in appearance. In some specimens it is missing, in others it is only a short bar not visibly connected with the ocular ridges; a few specimens only show the connexion of the band with the ocular ridges. Similar observations have been made on other Middle Cambrian ptychopariids from Australia. The parafrontal band is as narrow as the ocular ridge with which it is connected, and presumably functioned as a duct connecting the left and the right genal caecal glands. It had, perhaps, the special function of maintaining, for example, the equality of pressure in the cheeks and the eyes. The variable external appearance of the parafrontal band indicates that the depth of the duct in the tissue varied from one individual to another.

The ocular ridges are double. Each ridge consists of an anterior and a posterior band or ridge; both hands extend into the palpebral lobe, which is also double, and consists of an outer and an inner lobe. Running lengthwise between the anterior and posterior ocular ridges and the outer and inner palpebral lobes is a furrow—the ocular striga. The striga is a furrow within the palpebral lobe, and should not be confused with the actual palpebral furrow that separates the whole palpebral lobe from the fixed cheek.

The ocular ridges and the inner palpebral lobes are major diverticula (diverticular trunks). From the anterior ocular ridges and the parafrontal band arise the caeca of the brim, including the marginal frontal border, and the caeca of the anterior fields of the cheeks. From the inner edge of the posterior ocular ridge (and its extension—the inner palpebral lobe) caeca arise and merge with the ramification of the propleural caeca.

The edge of the palpebral lobe is defined by the facial suture; but it is assumed that this lobe contains an ingluvies from which (from the base of the eye outside the suture) the caeca of the free cheeks arise.

The alimentary prosopon of the cephalon of *Papyriaspis* as described above requires further interpretation. Thus, the paired ocular ridges are probably homologous with the paired caecal veins of the occipital segment and with the intestinal appendages of the thoracic segments; if so, the ocular strigae are homologous with the pleural furrows, and the palpebral lobes with the opistopleural terminal swelling at the tips of the pleurae.

Since the ocular strigae divide the palpebral lobe into two parts, a second explanation is possible. It is, however, much more complicated, and therefore less probable than the first. Each part of the palpebral lobe, perhaps, is a separate opistopleural swelling, and the ocular ridges should therefore each be an opistopleural diverticulum; if so, the intervening striga should be a segmental joint replacing the obsolete propleuron of the posterior segment. It should, however, be noted that, so far as is known, even three pairs of ocular ridges may represent a single segment, because the opistopleuron contains two veins (including the subsidiary vein).

The visual faces of the eyes have, of course, no inherent connexion with the alimentary apparatus except for the support given by the ingluvial buttresses, which are located in the cavities of the palpebral lobes. The palpebral lobes are surrounded by radiating caeca, and each lobe being a source of caeca certainly contained a diverticular ingluvies.

Weighing the probable explanations, preference should be given to the simpler alternative. It is, therefore, fair to conclude that each eye is situated at a pleural tip, and its position corresponds to that of the opistopleural terminal swelling.

If the classification of eyes by Raw (1956; 1957) is accepted, the eyes of *Papyriaspis*

should be classed as segmental. The opistopleural terminal swellings may indicate vestiges of completely obsolete eyes that 'were apparently in the pro-Arthropod borne on the pleura' (1956, p. 679).

The swellings on the posterolateral limbs of *Papyriaspis* and on the pleural tips of its thorax are blind, but the blindness by itself justifies no conclusion that eyes are 'lost' or that such eyes may not have existed at all in the ancestors. It is, nevertheless, safe to assume that the opistopleural swellings are ingluvial expansions of intestinal append-ages similar to the palpebral lobes, and that the swellings and the lobes have a homo-logous position; but it is just as speculative to assume the loss of corresponding eyes as to say that these swellings were about to develop visual surfaces of their own.

## THE PYGIDIUM OF A PTYCHOPARIID

Plate 69, fig. 2; text-fig. 14

The illustrated pygidium belongs to an undescribed genus from the early Upper Cambrian of Queensland. The ramified pattern of the anterior pleural veins (intestinal appendages) changes into a reticulate pattern at the rear of the pygidium. Behind the axial terminus strong median ramified caeca can be seen. The doublure is narrow and the axis short, as if its actual terminus is concealed under the test. Behind the terminus the test is swollen and forms a shallow boss.

It is improbable that the median terminal caeca arise from the anal segment, and it is, therefore, reasonable to assume that the axis actually extended below the dorsal test into the 'boss' as a testless terminus which may have contained the end segment.

PLEURA OF *CENTROPLEURA*

Plate 68, figs. 3, 4; text-fig. 13

One of the illustrated pleurae (fig. 4) belongs to the foremost segment of a *Centro-pleura* from the Middle Cambrian Devoncourt Limestone of Queensland and is ex-plained in text-fig. 13. The pleura is narrow and relatively long and shows strong
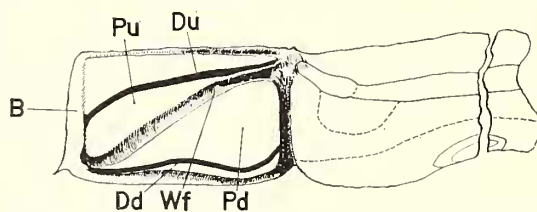
TEXT-FIG. 13. *Centropleura*. Pleura (Pl. 68, fig. 3). B—border with doublure; Dd—opistopleural vein (intestinal appendage); Du—propleural vein (intestinal appendage); Pd—opistopleuron; Pu—pro-pleuron; Wf—pleural furrow.

propleural and opistopleural veins. The specimen is a rubber cast of the internal face of the test on which the outer ornamental lines are only partly reflected. Externally (as seen in the other pleura—Pl. 68, fig. 3) the ornamental lines are strong and the opisto-pleural vein only is slightly indicated. The pleura of *Centropleura* has a remote and superficial similarity to a truncated insect wing.

CONCLUSIONS

1. The alimentary prosopon of agnostids, *Olenellus*, and *Redlichia*, ptychopariids, and *Centropleura* reflects the pleural alimentary apparatus. The surveyed data belong to various and representative families, and the results should be valid for agnostids and for Cambrian opisthoparian trilobites. Post-Cambrian Opisthoparia probably differ little from the Cambrian Opisthoparia in principle. This inference is based on the general morphological similarity of Cambrian and post-Cambrian trilobites, and on phylogenetic considerations. No observations are available for Cambrian eodiscids and post-Cambrian proparian trilobites.

2. Agnostids, *Redlichia*, and *Olenellus*, and ptychopariids represent three different groups with respect to the form of their caecal glands.

Agnostids have dendritic caecal glands with relatively few ramifications; the diameters of single caeca exceed capillary size; their diverticula are short ducts. Caeca of capillary size have not been observed in agnostids.

Redlichia and *Olenellus* have capillary ramified radiating and reticulate caeca on the cheeks (including the brim), and probably two to four pairs of sac-like ingluvies in the fixed cheeks and palpebral lobes.

Ptychopariids have capillary caeca that branch to form a reticulate pattern. The cephalic diverticula of ptychopariids consist of ramified bundles of caecal veins.

TEXT-FIG. 14. Pygidium of a new genus of ptychopariids. Semi-diagrammatic tracing of the specimen figured on Pl. 69, fig. 2. Aa—articulating half-ring; B—border with doublure; fi—interpleural groove; Nf—articulating furrow; R—reticulate caeca ('genal caeca'); Wf—pleural furrow.
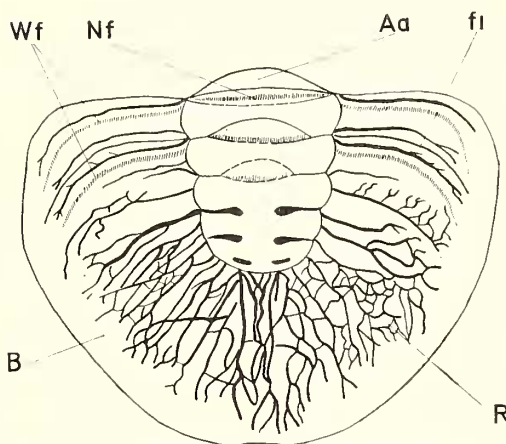
3. Alimentary appendages (diverticula and caeca) are not confined to the cephalon. They are present in each segment of the thorax and pygidium in the form of intestinal appendages. Their distribution and arrangement are segmental.

4. In *Redlichia*, *Centropleura*, ptychopariids, and olenids, each segment of the thorax bears two pairs of lateral intestinal appendages, one pair in front of and another behind the pleural furrows.

5. In ptychopariids the paired intestinal appendages of the posterior, fused, portion of the pygidium develop a type of reticulation similar to that of the genal caeca.

6. In the ptychopariid *Papyriaspis*, swellings at the pleural tips of the anterior thoracic segments and the tips of the posterolateral limbs connect with the opistopleural caecal vein. These swellings probably functioned as glands.

7. The ocular ridges of *Papyriaspis* consist of two parallel ridges each of which passes into the palpebral lobes; the ocular ridges are probably homologous with the pleural intestinal appendages and constitute a single segment; the palpebral lobes and the eyes are situated at the tips of the segment represented by the ocular ridges. The cephalic eyes are, consequently, segmental eyes.

8. The palpebral lobes (with the cephalic eyes) and the opistopleural glandular swellings have homologous positions within their segments; the opistopleural swellings, therefore, may represent vestiges of pleural eyes; or the palpebral lobes (excluding the eyes) and the opistopleural swellings may be homologous, or may contain homologous organs. Any of these alternatives is reasonable because the cephalic eyes and the palpebral lobes to which the eyes adhere are different and unrelated organs and may have followed independent trends in their history.

9. The caecal prosopon occurs only on the pleural lobes of the trilobite and is not observed on the axial lobe; ramification and reticulation of caeca develop concurrently with the fusion of pleurae. Consequently, the frontal border, consisting of brim, rim, and doublure, comprises fused pleurae. This conclusion is supported by the observation that in all trilobites the sutures are confined to the pleural lobe (Öpik 1958, p. 29). Moreover, 'all axial parts of the tergum are surrounded by pleurae' (loc. cit.); the pleural doublure is continuous and the frontal doublure together with the rostral shield is a part of it.

10. The pleurae that are contained in the frontal border and the free cheeks probably belong to the segments that are indicated in the glabella; there is no evidence to indicate that the frontal border contains any other segments. These pleurae intervene between the axial lobe (glabella) and the ventral hypostoma (see Öpik 1958, p. 30).

DESCRIPTION OF *GLYPTAGNOSTUS*

GLYPTAGNOSTUS Whitehouse 1936

Plate 70; text-figs. 15, 16

Species of Glyptagnostus. The type species is *G. toreuma* Whitehouse 1936. According to Westergaard (1947, p. 5) *G. torenma* is synonymous with *G. reticulatus* (Angelin 1851), and so is *G. angelini* Resser 1938. Kobayashi (1949) supports this interpretation. The synonymy is subjective and reflects the present state of knowledge of these forms. *G. reticulatus nodulosus* Westergaard 1947 completes the specific list of the genus. A new species—*Glyptagnostus stolidotus*—is described below.

Concept of the genus. The reticulate or blistered surface of the test has been regarded as the main diagnostic character of the genus. The distribution, size, and number of the blisters are highly variable and provide no specific criteria. An exception is *G. reticulatus nodulosus* Westergaard, a subspecies with an 'over-blistered' cephalon and an 'under-blistered' pygidium, in which the radiating and furcating rugae have preserved their continuity.

The inclusion of the non-reticulate new species *stolidotus* in *Glyptagnostus* necessitates a modification of the generic concept and a re-evaluation of the generic significance of the 'blisters'.

The reticulation (blistering) is created by scrobicules crossing the rugae. Most of these cross-scrobicules are shallow and many are incomplete. In such cases (see, for example, Westergaard 1947, pl. 1, fig. 8) the rugae are laterally notched. In the new *G. stolidotus* laterally notched rugae also occur, but no complete blisters are present. It appears, therefore, that blistering or reticulation is the specific character of *G. reticulatus* and its

subspecies, but it cannot be regarded as a generic character. Nevertheless, the genus *Glyptagnostus* is not invalidated by such an interpretation.

The main diagnostic character of *Glyptagnostus* is the presence of rugae (and scrobicules) on both cephalon and pygidium. In the pygidium six or seven pairs of first-order rugae are present; they fork to form about twice as many second-order rugae, which in larger specimens themselves fork and produce short rugae (terminal caeca) of the third order. In the cephalon about ten pairs (nine to eleven) of first-order caeca (rugae) are present, and their number multiplies by forking into rugae of the second and third orders. A similar number of caeca (rugae) is seen in *Diplagnostus* (text-fig. 2), but the pattern in *Glyptagnostus* is that of a *Ptychagnostus* with a pair of arcuate scrobicules (text-fig. 4*b*).

The structure of the glabella and the pygidial axis (text-fig. 15) supplements the generic diagnosis of *Glyptagnostus*. The glabella is distinct in having a sub-pentagonal flattened anterior lobe with a bifurcate sulcus, and two pairs of lateral lobes including the basal lobe. Among agnostids with scrobiculate cephala *Lotagnostus* Whitehouse (1936) alone has a similar glabella.

The structure of the median sulcus in *Glyptagnostus* is unique, but is rarely well preserved. It consists of a deep notch in the middle of the frontal lobe and an oval depression which may even reach the transverse furrow. It is illustrated, for example, by Westergaard (1947, pl. 1, fig. 5).

The pygidial axis is trifid, with a median train of three unequal 'bulbs', the anterior of which carries the blunt axial spine with a superimposed small node. The median train of bulbs is flanked by a pair of depressed areas bounded by shallow, incised dorsal furrows. In these depressions, in the best-preserved specimens, seven pairs of pits (muscle spots, apodemes) can be observed (Pl. 70, fig. 9). They are also illustrated by Westergaard (1947, pl. 1), and so is the small median terminal node on the second axial 'bulb'.

The term 'bulb' (or 'axial bulb') indicates that these features do not correspond exactly to, and are therefore distinct from, segmental axial lobes.

The pygidial axis is also quadrilobate, with three discontinuous transverse furrows. The three anterior axial lobes are of about equal size and occupy the anterior half of the axis. The fourth lobe forms the posterior half of the axis, carries the two posterior 'bulbs', and is pointed at the rear. The articulating furrow is wide and deep, the articulating half-ring narrow and elevated.

As regards a similarity with *Lotagnostus* more comment is needed. The species referred to are: *Lotagnostus trisectus* (Salter) (Westergaard 1922, pl. 1, fig. 11), *L. trisectus* mut. *ponepunctus* (Matthew) (1903, pl. 17, fig. 8), *Agnostus americanus* Billings (Rasetti 1944, pl. 36, figs. 1, 2), *Lotagnostus asiaticus* Troedsson 1937, and *Lotagnostus obscurus* Palmer 1955.

In all these species the pygidial articulating furrow is narrow (normal); the axis is tripartite longitudinally and trilobate transversally and laterally not depressed, but swollen; and the number of first-order rugae (where they are discernible) is visibly greater than in *Glyptagnostus*. Moreover, only one pair of lateral lobes (the basal lobes) is present in the glabella of *Lotagnostus*.

Diagnosis. Cephalon and pygidium rugose (scrobiculate); about ten pairs of cephalic and six or seven pairs of pygidial first-order caecal rugae; arcuate scrobicules in cephalon; two pairs of glabellar lateral lobes including basal lobes; pygidial axis trifid with a

median train of three unequal 'bulbs', the anterior 'bulb' with axial spine (node); lateral axial depressions with about seven pairs of pits (muscle spots); three anterior axial lobes, three discontinuous transverse furrows, and a large pointed terminal lobe; articulating furrow deep and wide. The type species has reticulate rugae.

Stratigraphic distribution in Queensland. G. stolidotus is the oldest known species. It occurs in beds which can be correlated with the upper half of the Scandinavian Upper Cambrian zone with *Agnostus pisiformis*. *G. stolidotus* has been found in numerous out-crops of the Georgina Limestone (lower levels), the Pomegranate Limestone (lower horizon on Wills Creek), and the O'Hara Shale ('lower O'Hara fauna').

    G. reticulatus follows *stolidotus* immediately in time. Apparently the life-spans of the two species overlap for a short interval (represented by a few feet of sediment only). *G. reticulatus* occurs in Queensland in two separate successive horizons.

    In the lower horizon, immediately above *stolidotus*, *G. reticulatus* is associated with *Olenus* at Pomegranate Creek, and with some of the latest genera of the 'lower O'Hara fauna' at Wills Creek. The complete specimens (Pl. 70, figs. 10, 11) came from this locality. In the upper horizon, which is known from many localities of the Georgina Limestone, *G. reticulatus* is associated with species of *Pseudagnostus*, *Proceratopyge*, and *Eugonocare*, as described by Whitehouse (1936; 1939). This horizon corresponds to the '*Glyptagnostus* stage' of Whitehouse, from which *G. toreuma* was described. These two horizons with *Glyptagnostus* can be correlated with the three lowermost subzones of the Scandinavian *Olenus* zone, which also contain *G. reticulatus* (Westergaard 1947). Explanations of the geographical and geological names used above are found in Öpik (1956; 1960).

Phylogeny. The early specimens of *G. reticulatus* and its late representatives described as *G. toreuma* are very similar, and the derivation of *toreuma* is in no need of discussion. *G. 'toreuma'* is distinguished by the abundance of very large specimens in its population.

    G. stolidotus antedates *reticulatus* in every locality and may be interpreted as the ancestor of *reticulatus*. If so, Queensland should be the centre from which *Glyptagnostus* spread over the Cambrian seas of the world—a conclusion that is not supported by other evidence. It is evident, also, that *G. reticulatus* and *stolidotus* are different in the structure of the pygidial axis and are quite distinct species without intermediate links in Queensland. It should be assumed, therefore, that *stolidotus* is not itself the immediate ancestor of *reticulatus*, but is still very close to the unknown actual progenitor of *reticulatus*.

    The origin of *G. stolidotus* itself is not evident. The structure of its glabella, pygidial axis, and cephalic caeca indicates relationship with the Middle Cambrian *Ptychagnostus*, but none of the known species of the latter is close enough to be considered a direct ancestor of *Glyptagnostus*.

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Glyptagnostus reticulatus (Angelin)

Plate 70, figs. 9–11; text-fig. 15

</div>

    The illustrated specimens come from two different localities and horizons. The specimen illustrated on Plate 70, fig. 9 (CPC 587) is from the Georgina Limestone (Locality W157), from the highest level of the occurrence of *Glyptagnostus reticulatus*, described as

G. toreuma Whitehouse. The pygidium illustrated here is identical with the holotype of *toreuma*, which is also a pygidium. It is 6·3 mm. long (without the articulating half-ring) and 6·5 mm. wide. It shows the small node on the axial spine and the terminal node on the middle axial bulb. Notable are the elevated rugae of the main caecal trunks (for explanations of terms, see text-fig. 16) flanking the axis, similar to the trunks of *stolidotus* (Pl. 70, fig. 3).

The two complete specimens (Pl. 70, figs. 10, 11) are from the same limestone bedding plane from Wills Creek (Loc. D126) and represent the lower horizon of the beds with
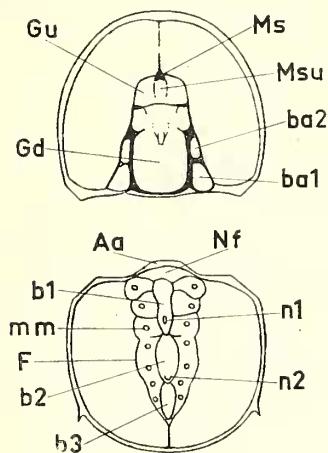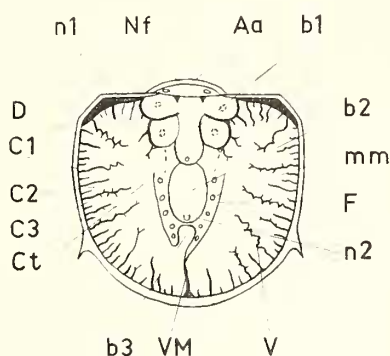

FIG. 15   FIG. 16

TEXT-FIG. 15. *Glyptagnostus reticulatus* (Angelin). Diagrams snowing the structure of glabella and pygidial axis. The reticulation is omitted (see Pl. 70, figs. 9–11) to facilitate comparison of axial structures of *G. reticulatus* and *G. stolidotus* (text-fig. 16). The pygidium represents a specimen from Pomegranate Creek with exceptionally well-preserved muscle spots (pits). *Cephalon*: ba1—basal lobe; ba2—lateral glabellar lobe; Gd—posterior lobe of glabella; Gu—anterior lobe of glabella; Ms—frontal sulcus; Msu—depressed extension of frontal sulcus. *Pygidium*: Aa—articulating half-ring; b1—anterior bulb; b2—middle bulb; b3—posterior bulb; F—dorsal (axial) furrow; mm—muscle spots (pits); n1—node on axial spine; n2—terminal axial node; Nf—articulating furrow.

TEXT-FIG. 16. *Glyptagnostus stolidotus* sp. nov. Diagram of pygidium. Aa—articulating half-ring; b1—anterior bulb; b2—middle bulb; b3—posterior bulb; C1—first-order caecum; C2—second-order caecum; C3—third-order caecum; Ct—main caecal trunk; D—diverticulum; F—dorsal (axial) furrow; mm—muscle spots (five posterior pairs—'pits'; two anterior pairs—'spots'); n1—tip of axial spine (node); n2—terminal axial node; Nf—articulating furrow (with a pair of muscle pits or appendiferi); V—lateral scrobicula; VM—median scrobicula (postaxial median furrow).

Glyptagnostus reticulatus. The larger specimen (CPC 588), 11·4 mm. long and 5·4 mm. wide, has about the same number of blisters on the cephalon and pygidium, whereas in the smaller specimen (CPC 589), 8·4 mm. long and 3·9 mm. wide, the pygidium has visibly fewer blisters than the cephalon. This is an example of the variability of the reticulation already indicated in the discussion of the genus.

Diagnosis. Test rugose, rugae reticulate (blistered); outline of cephalon subelliptical, node on posterior glabellar lobe, on its anterior half, elongate and relatively prominent; anterior half of pygidial axis divided by discontinuous transverse furrows into three lobes; anterior lobe of pygidial axis tripartite, low node superimposed on axial spine;

posterior bulb of axis relatively long (about one-quarter of axial length), middle bulb narrow (about one-fifth of axial length); seven pairs of muscle spots (pits of even depth) in axis.

Glyptagnostus stolidotus sp. nov.
Plate 70, figs. 1–8; text-fig. 16

Diagnosis. Rugose, without blisters (except for occasional blisters on cheeks near the basal lobes); outline of cephalon subcircular, small rounded central node on posterior glabellar lobe; two anterior axial lobes on pygidium defined by discontinuous transverse furrows, a third lobe occasionally indicated; anterior lobe of pygidial axis undivided, or tripartition indicated occasionally by vestigial furrows; posterior bulb of pygidial axis small (one-eighth of axial length), middle bulb wide (one-third of length of axis); five posterior pairs of muscle spots on pygidium as deep pits, two anterior pairs occasionally discernible as 'spots' only.

Holotype. The cephalon, CPC 584 (Pl. 70, fig. 6), from Loc. B525 at Wills Creek, Boulia area. A cephalon is selected as the holotype to facilitate comparison with the lectotype of *Glyptagnostus reticulatus* (Angelin) in Westergaard (1947, pl. 1, fig. 2), which is also a cephalon.

Comment on illustrated material. All the illustrated specimens have been collected from a single bed, which contains only one kind of cephala and of pygidia; it is therefore certain that the shields are conspecific, and that the material in hand represents a population within narrow limits. The collecting points are recorded as B525 and B537, which are about a quarter of a mile apart. Twenty-five cephala and fifteen pygidia were selected for examination.

The small pygidium (Pl. 70, fig. 1; CPC 579) is 4·8 mm. long and 5·0 mm. wide. Third-order caeca are present; they are uncommon in such small specimens.

The fragmentary pygidium (Pl. 70, fig. 2; CPC 580) is 5·9 mm. long. The diverticula are separated from the axial lobe by a shallow furrow. Third-order caeca are numerous. The posterior bulb is small and is connected with the left gland.

Another fragmentary pygidium (Pl. 70, fig. 3; CPC 581), the largest found, is 6·1 mm. long. It is photographed with a tilt to the right to show the gland in a horizontal plane. Third-order caeca are numerous; the posterior bulb is visibly part of the left gland. The edges of the anterior caeca are serrate. The main caecal trunks flank the axis as prominent ridges, as is also indicated in the pygidium of *G. reticulatus* (Pl. 70, fig. 9). On the end of the middle bulb the tiny terminal node is preserved, just as in fig. 9.

EXPLANATION OF PLATE 70

All specimens ×6

Figs. 1–8. *Glyptagnostus stolidotus* sp. nov., Upper Cambrian Pomegranate Limestone, lower horizon at Wills Creek, Boulia area, western Queensland. Fig. 6 (holotype cranidium) from Loc. B525 (CPC 584); all other specimens Loc. B537. 1, CPC 579; 2, CPC 580; 3, CPC 581; 4, CPC 582; 5, CPC 583; 7, CPC 585; 8, CPC 586.

Fig. 9. *Glyptagnostus reticulatus* (Angelin), pygidium, Upper Cambrian Georgina Limestone; Loc. W157, south of Glenormiston, western Queensland. (CPC 587.)

Figs. 10, 11. *Glyptagnostus reticulatus* (Angelin), Upper Cambrian Pomegranate Limestone, upper horizon at Wills Creek, western Queensland. Loc. D126. 10, CPC 586; 11, CPC 589.
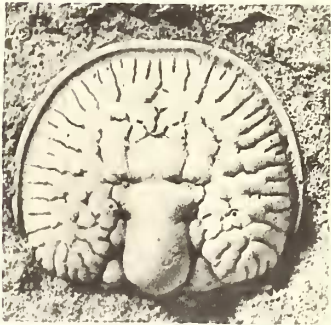
ÖPIK, Upper Cambrian trilobites